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**Resilience of inshore, juvenile snapper *Pagrus auratus* to angling and release**

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Suggested running headline: Post-release mortality of *Pagrus auratus*

## Abstract

This study assessed the mortality of 157 snapper *Pagrus auratus* (9–29 cm  $L_T$ ) after being conventionally angled and then released into cages (along with 48 controls) for 4 days off southeastern Australia. Fatalities were restricted to 12 angled fish (7.6%) and mostly attributed to the ingestion of hooks and especially their subsequent removal, which caused substantial blood loss and immediate death. Hook ingestion was significantly biased towards smaller fish (<21 cm  $L_T$ ) and attributed to a lower chance of anglers initially detecting these individuals on the line (allowing them to consume more of the baits). While mortalities might be reduced in future via (1) choosing terminal rigs that promote mouth hooking and/or (2) cutting the line on any-hook ingested fish, the results nevertheless validate releasing unwanted angled inshore juvenile *P. auratus* as a means for managing their exploitation.

Key words: catch-and-release; hook ingestion; post-release mortality; Sparidae.

## INTRODUCTION

Sparidae encompasses more than 33 genera and 110 species, with a global distribution across tropical and temperate estuarine and coastal demersal areas (Carpenter & Johnson, 2002). Many sparids are economically important and form the basis of important artisanal, commercial and, in developed countries, recreational fisheries (Broadhurst *et al.*, 2005; Götz *et al.*, 2007; Alós *et al.*, 2008; Overton *et al.*, 2008; Veiga *et al.*, 2011).

At least ten sparids (six genera) occur in Australia (Carpenter & Niem, 2001; Grant, 2008); all of which are recreationally fished for an estimated annual catch of almost 17 million individuals (Henry & Lyle, 2003). The exact catch composition is unknown, but the most abundant species include *Acanthopagrus* spp. [especially yellowfin bream *A. australis* (Owen 1853) and black bream *A. butcheri* (Munro 1949); *c.* 50% of the total] and snapper *Pagrus auratus* (Bloch & Schneider 1801) (*c.* 20%) (estimated in 2000/01 by Henry & Lyle, 2003). Like most recreationally targeted sparids throughout the world (*e.g.* those described by Götz *et al.*, 2007; Alós *et al.*, 2008; Overton *et al.*, 2008; Veiga *et al.*, 2011), the Australian species are managed by legal sizes and personal quotas. Combined with voluntary non-consumptive fishing, these regulations result in *c.* 11 million sparids (65% of the total catch) being released per annum; which is among the greatest rate for any family of Australian teleosts (Henry & Lyle, 2003).

Recognition of the need to validate the assumption of few negative impacts to such large numbers of released fish has resulted in several relevant studies, and mostly for *A. australis* (Broadhurst *et al.*, 1999, 2005, 2007; Butcher *et al.*, 2007, 2008, 2010; Reynolds *et al.*, 2009) and *A. butcheri* (Haddy & Pankhurst, 1999, 2000; Grixti *et al.*, 2007, 2008). This

work estimated total short-term (<10 days) mortalities of <28% for both species and, like for virtually all other studied sparids (e.g. Götz *et al.*, 2007; Rudershausen *et al.*, 2007; Overton *et al.*, 2008; Alós *et al.*, 2009a; Veiga *et al.*, 2011), identified hook ingestion as a consistent, key deleterious factor (Broadhurst *et al.*, 2005; Gixti *et al.*, 2008). Consequently, most efforts at mitigating mortalities have concentrated on promoting shallow hooking, via modifications to terminal rigs and/or fishing methods (Gixti *et al.*, 2007; Butcher *et al.*, 2008, 2010).

Much less information is available on the post-release fate of the remaining Australian sparids, including the highly valued *P. auratus*. Such bias can be partially attributed to comparatively lower catch and release, although species-specific distributions and the logistics of assessing mortality are also important. For example, *A. australis* and *A. butcheri* tolerate a wide range of salinities and occur in coastal rivers, estuaries and near shore areas in large abundances and across all sizes (Grant, 2008). In contrast, *P. auratus* prefer marine waters with juveniles and small adults (< c. 40 cm  $L_T$ ) mostly located in shallow bays, while larger fish are often distributed across the continental shelf down to 200 m (Sumpton *et al.*, 2003; Grant, 2008). The cheapest field-based experiments to assess short-term post-release mortality involve angling fish and then ‘releasing’ and monitoring them in replicate, large surface cages (termed ‘confinement’ studies; Pollock & Pine, 2007); which need to be moored close to the fishing area, and in low flow with protection from waves. Such logistical requirements have been more suited to the distributions of *Acanthopagrus* spp.

Notwithstanding the above, two short-term confinement studies involving *P. auratus* have been published in the primary literature (Broadhurst *et al.*, 2005; Gixti *et al.*, 2010a). Both have estimated mortalities to juveniles, but with various limitations. Specifically,

Broadhurst *et al.* (2005) t-bar tagged 72 angled fish (15–31 cm  $L_T$ ) in Botany Bay, New South Wales (NSW) and released them along with controls (caught by seining) into four floating 48 000 l cages for 10 days. Although catch histories were available for each angled fish, there were insufficient numbers and/or data to attribute causality among the observed fatalities (c. 33%). Grixti *et al.* (2010a) followed a similar design in Port Phillip Bay, Victoria, but instead of being tagged, 620 fish (15–26 cm  $L_T$ ) were fin clipped according to intuitive *a priori* treatments and monitored for either 1 h or 3 days. This experimental approach facilitated relative mortality assessments (e.g. between shallow- and deep-hooked fish of 3 and 52%) but, because individual fish could not be identified, precluded quantifying the full range of contributing factors, including any random effects.

Isolating the key deleterious impacts associated with angling (and their mechanisms of action) is important to prioritise resolution strategies. This study aimed to acquire such information for inshore juvenile *P. auratus* by collecting detailed data describing their conventional angling and handling across a sufficient sample size, and then immediately releasing them individually (or at densities where they could be subsequently identified by their  $L_T$ ) into cages; most of which were rigid and submerged to the seabed (< 10 m depth) where they were protected from tide and wave action.

## MATERIALS AND METHODS

Twenty-four boat-based anglers were asked to target *P. auratus* between 06:00 and 14:00 on one day during January 2008 in Botany Bay, NSW (34.0° S; 151.2° E), and then immediately place their fish into portable 110 l cylindrical cages (provided by researchers) tethered to their boats. The cages were made from polyvinyl chloride (PVC) buckets with

lids, and comprised one top and two lateral ‘windows’ positioned at 300 mm above the base (with a combined area of *c.* 1200 cm<sup>2</sup>) and covered by 6-mm PVC mesh. Depending on their sizes, *P. auratus* were caged at densities of 1–10 so that the total weight was <5 kg 110 l cage<sup>-1</sup>. Anglers completed a data sheet for each fish and placed it into the 110 l cage before securing the lid and alerting researchers.

Researchers retrieved the 110 l cages and, after removing the datasheets and checking for deaths, transported them to a monitoring site, comprising two 240 m lengths of 12 mm diameter (Ø) polyamide (PA) rope buoyed at the surface in a straight line (anchored at either end). The 110 l cages were weighted (2 kg brick), tied to the 12 mm Ø rope at 5 m intervals and deployed to the sea bed (3 m). When all of the available 110 l cages (*n* = 78) were stocked, angled *P. auratus* were still collected as above, but then transferred to one of three 2600 l cylindrical floating cages (made from 22 mm PA mesh attached to PVC frames) deployed on the surface between the monitoring sites. All multi-stocked *P. auratus* were identified by *L<sub>T</sub>*.

After the angled fish were caged, 48 ‘control’ *P. auratus* that were previously trapped or angled in shallow water off Coffs Harbour (30.3° S; 153.1° E), and housed in aquaria for three months were distributed among 41 empty 110 l cages (at comparable stocking densities as the angled fish) and similarly deployed at the monitoring sites on the same day. The controls were handled, transported and housed according to the methods described by Broadhurst *et al.* (1999).

All cages were retrieved after four days and any mortalities were recorded. At this time, 10 angled and 11 control *P. auratus* were randomly selected from their cages and



sampled for blood within 1 min of initial disturbance following the methods outlined by Broadhurst *et al.* (2005). Eleven *P. auratus* were also angled from Botany Bay and similarly sampled (within 1 min of hooking).

## DATA COLLECTED AND ANALYSES

The following general categories of data were collected for all angled *P. auratus*: angler name; hook type and size (absolute; mm<sup>2</sup>); line strength (kg); trace length (cm); bait and rig types; whether the boat was anchored or drifting; fishing depth (m); period between hooking and landing (*i.e.* playing time in s); landing and restraint methods; period of air exposure during unhooking and ‘release’ (s); anatomical hook location; whether or not the hook was removed;  $L_T$  (cm); the presence or absence of fin damage, scale loss, bleeding or hook damage; cage number; and whether they died or survived the experiment. Replicate water temperature (°C) and dissolved oxygen (mg l<sup>-1</sup>) were recorded on the fishing and monitoring days using an Horiba U/10 water quality meter.

A Fisher’s exact test was used to test the hypothesis of no difference in the total numbers of angled and control *P. auratus* surviving at the end of the experiment. All data describing the capture and handling of each angled fish were collated as either fixed ‘terminal-rig’, ‘fishing-and-landing’ or ‘angling-response’ factors. Design factors (considered as being random) included ‘anglers’ and ‘cages’. These various terms were then considered for inclusion in generalised linear mixed models (GLMMs) fitted using ASReml-R (Butler *et al.* 2009) and via penalized quasi-likelihood (Breslow & Clayton, 1993) to the dichotomous status (alive *v.* dead) of *P. saltatrix* at the end of the experiment. Total length was included as a co-variate in all models.

163

164       After assessing the baseline model, two groups of GLMMs were separately fitted using a  
165 forward selection approach to ascertain which of the (1) terminal-rig and fishing-and-landing  
166 or (2) angling-response factors contributed towards fatalities. Where appropriate, significant  
167 fixed effects identified in these analyses were then considered as response variables and  
168 GLMMs fitted to isolate their causes. This sequential and structured modelling approach is  
169 biologically plausible and avoids many of the statistical challenges and pitfalls associated  
170 with variable selection in GLMMs for small data sets. But, the limited sample size and low-  
171 frequency binary data mean that all modelling should be considered descriptive, rather than  
172 predictive.

173

174       The *P*-values for the various GLMMs were derived via the asymptotic distribution of two  
175 test statistics: (1) a pseudo *F*-to-enter based on a Wald value (from the GLMM), and (2) the  
176 change in deviance from a generalised linear model obtained by excluding the random terms.  
177 Both approaches were chosen to overcome inherent technical problems. In particular, the  
178 Wald test suffers from the Hauck-Donner phenomenon (Hauck & Donner, 1977), while using  
179 the change in model deviance to derive *P*-values can be anti-conservative if there is  
180 significant extra-binomial variation induced by ignoring sources of variation from the random  
181 terms.

182

183       The blood samples were analysed for concentrations of cortisol (ng ml<sup>-1</sup>) and plasma  
184 glucose (mM) by direct chemiluminescent immunoassay and using an enzymatic  
185 spectrophotometric assay, respectively, according to the manufacturers' instructions. Owing  
186 to low levels of both parameters (below the detectable range – see Results) among baseline  
187 and control fish, formal statistical analyses were not done to test the hypothesis of no

differences among the groups of fish. Rather, the extent of censored data and mean levels of both parameters for which there were recordable data are presented.

## RESULTS

In total, 157 *P. auratus* (mean  $L_T \pm$  S.D. of  $18.4 \pm 4.2$  cm) were caught by 15 of the 24 anglers using various terminal rig configurations (but all comprising baited, J or circle hooks), played for mostly <1 min, and then, within an additional 1 min, typically landed without a net, restrained by hand while the hook was either removed (most fish) or the line cut, and released into the cages (Table I). Of these fish, 150 were subsequently deployed and monitored alongside the controls ( $25.8 \pm 2.4$  cm  $L_T$ ). Water temperature (mean  $\pm$  S.D. of  $22.5 \pm 0.4^\circ\text{C}$ ), salinity ( $36.0 \pm 0.0$  psu) and DO ( $8.5 \pm 0.4$  mg  $\text{l}^{-1}$ ) remained similar during the angling and subsequent monitoring days.

## FATALITIES AND CAUSES

There were no fatalities among the controls, but seven of the angled *P. auratus* died immediately after being placed in the cages (and prior to their deployment—within 5 min of capture), while another five fish were dead at the end of the monitoring period, providing a total, non-significant anger-induced mortality of 7.6% (Fisher's exact test,  $P > 0.05$ ). The initial fatalities and solitary confinement of most fish precluded the coherent inclusion of cages as a random term; restricting the baseline model to the intercept and random effect of anglers.

Because nine of the 12 fatalities were caught by two of the 15 anglers, this term explained nearly 30% of the total variation in the baseline model, although the residual also clearly indicated the influence of other factors. The first GLMMs fitted to those fixed factors describing the terminal rig and fishing and landing processes (and with  $L_T$  as a co-variate) identified that only hook removal was significant, with both  $P(\text{Wald and deviance}) < 0.01$  (Tables I and II). But this treatment was clearly confounded by anatomical hook location, with hooks removed from all 142 mouth-caught individuals (with only two deaths), but left in 11 hook-ingested fish (of which six died) and removed from three (all died). No other variables, including the  $L_T$  of fish were significant after hook removal was included as a term and the model refitted ( $P > 0.05$ ; Table II).

The importance of anatomical hook location in determining fatalities (*i.e.* nine of 14 hook-ingested v. two of 142 mouth-hooked fish; Table I) was subsequently explored in the second group of GLMMs assessing the influence of just the angling-response factors. Both this factor and bleeding were the only significant main effects; returning  $P < 0.01$  for both the Wald and change in deviance test statistics (Table II). However, all of the bleeding fatalities (four of 12 inflicted fish; Table I) had ingested their hooks, suggesting some co-dependency between anatomical hook location and the presence of blood. A GLMM refitted accounting for anatomical hook location supports this conclusion, with a  $P(\text{Wald}) < 0.05$ , but a  $P(\text{deviance}) > 0.05$  for bleeding. Subsequent assessment of the interaction between bleeding and anatomical hook location also returned conflicting levels of significance [ $P(\text{Wald}) > 0.05$  and  $P(\text{deviance}) < 0.05$ ]. These analyses, combined with a lack of any significant effects of  $L_T$  or hook damage ( $P > 0.05$ ; Table II), suggest that anatomical hook location was the most important predictor of fatalities.

Based on these results, anatomical hook location was then considered as a binary response variable (mouth v. ingested) and GLMMs fitted in an attempt to isolate explanatory factors (Table III). The only significant factor was  $L_T$ , which returned a  $P(\text{Wald}) < 0.01$ , but a highly non-significant  $P(\text{deviance}) > 0.05$  (Table III). Because the  $P(\text{deviance})$  ignores random effects, such disparity in significance indicated a strong dependency on angler. This relationship was explored in a conditional scatter (jittered) plot of anatomical hook location against  $L_T$  for each angler, which revealed that for most of the anglers ( $n = 9$ ) that caught hook-ingested fish, there was a bias towards this occurring among smaller individuals (Fig. 1).

#### PHYSIOLOGICAL RESPONSE OF ANGLED FISH

The chemiluminescent immunoassay was unable to detect plasma concentrations of cortisol  $< 3.6 \text{ ng ml}^{-1}$  among either those *P. auratus* that were immediately sampled after angling, or the caged controls ( $n = 11$  for both). Similarly, four of the caged angled fish had cortisol concentrations below the detectable range of the assay. The remaining six caged angled fish had a mean ( $\pm$  S.D.) concentration of  $4.3 \pm 0.4 \text{ ng ml}^{-1}$ . Comparatively fewer censored data were recorded for plasma glucose ( $< 1.0 \text{ mM}$ ) among baseline ( $n = 8$ ), controls (4) and angled (4) fish using the enzymatic spectrophotometric assay. The remaining means ( $\pm$  S.D.) were  $1.7 \pm 0.6$ ,  $1.9 \pm 0.3$  and  $2.2 \pm 0.6 \text{ mM}$ , respectively.

#### DISCUSSION

The c. 8% mortality of *P. auratus* in this study is lower than the c. 33% recorded by Broadhurst *et al.* (2005) for the same population, but comparable to Grixti *et al.*'s (2010a)

estimate of c. 11% (pooled across treatments) for more southern stocks. This estimate is also within the range of other sparids angled from the same depths (<10 m), including *A. australis* (5–28%; Broadhurst *et al.*, 2005; Butcher *et al.*, 2007), *A. butcheri* (8%; Grixti *et al.*, 2008), black seabream *Spondyllosoma cantharus* L. 1758 (2.8%; Veiga *et al.*, 2011), gilthead seabream *Sparus aurata* L. 1758 (11.7%; Veiga *et al.*, 2011), two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire 1817) (0%; 2011) and striped seabream *Lithognathus mormyrus* L. 1758 (33%; Alós *et al.*, 2009a). Further, like for many assessed sparids, including those angled from deep water and incurring the cumulative impacts of barotrauma (e.g. *C. laticeps* – Götz *et al.*, 2007; *P. pagrus* – Rudershausen *et al.*, 2007; Overton *et al.*, 2008 and annular seabream *Diplodus annularis* L. 1758 – Alós *et al.*, 2009a), a large proportion of the variability among mortalities to *P. auratus* here was explained by the anatomical hook location (Broadhurst *et al.*, 2005; Butcher *et al.*, 2007; Grixti *et al.*, 2008, 2010a; Veiga *et al.*, 2011). This factor manifested as disproportionately greater deaths among individuals that ingested hooks (64%) than those hooked in the mouth (1.4%); a relationship comparable to that (52 v. 3%) observed by Grixti *et al.* (2010a).

There are at least two factors contributing towards such apparent consistency in the importance of anatomical hook location in deciding the fate of sparids. First, in all of the above cited experiments fish were angled on hooks with natural baits. It is well established that such configurations typically are ingested at a greater rate than artificial baits or lures (Bartholomew & Bohnsack, 2005). Second, juvenile sparids (*i.e.* typically comprising the greatest proportion of released individuals) often school, which might increase competition for baits as a perceived source of food and therefore contribute towards an aggressive hooking response. Most sparids are targeted with constant tension on the line (termed ‘active fishing’, but see Alós *et al.*, 2009a) which usually limits the depth of hooking (Bartholomew &

Bohnsack, 2005; Grixti *et al.*, 2007, 2010a), so presumably those that manage to ingest hooks, do so with sufficient force to cause considerable damage. Such impacts are supported here by most of the hook-ingested *P. auratus* dying within 5 min, (four of which bled profusely), and similar rapid fatalities among hook-ingested *A. australis* angled across comparable space and time (Broadhurst *et al.*, 2005; Butcher *et al.*, 2007).

While anatomical hook location (and associated bleeding) explained most of the fatalities in this study, the deaths of two mouth-hooked *P. auratus* indicates the influence of at least some other impacts; albeit nowhere near the extent observed by Broadhurst *et al.* (2005). Two unexamined factors that might have contributed to more *P. auratus* dying during this earlier work were (1) relatively warmer water temperatures (mean  $\pm$  S.D. of  $24.1 \pm 1.5$  v.  $22.5 \pm 0.4^{\circ}\text{C}$  here) and (2) tagging. More specifically, previous research has identified positive relationships between temperature and post-release mortality for several species (reviewed by Bartholomew & Bohnsack, 2005; Arlinghaus *et al.*, 2007) which are often attributed to a range of physiological disturbances, including a greater metabolic rate and demand for oxygen (Pörtner, 2002). Further, although tagging did not cause mortalities among the controls monitored by Broadhurst *et al.* (2005) or similar-sized *P. auratus* in other studies (*e.g.* Quartararo & Kearney, 1996; Sumpton *et al.*, 2003), undoubtedly this would have had some cumulative impact on angling stressors. Either of the above factors ultimately could have contributed towards mortality. The potential for such effects illustrates the need to carefully design experiments and to collect sufficient data to attribute causality.

Irrespective of differences in results between the present and the earlier studies, it is clear from the data presented here and by Grixti *et al.* (2010a), that limiting hook ingestion in juvenile *P. auratus* would concomitantly reduce fatalities. In addition to actively fishing the

line (discussed above), several factors have been identified to affect hook ingestion among sparids, including  $L_T$ , the hook type (circle v. J-hooks) and mass/size, trace length and bait type (Götz *et al.*, 2007; Grixti *et al.*, 2007, 2008, 2010a,b; Alós *et al.*, 2008, 2009b,c; Butcher *et al.*, 2008; Veiga *et al.*, 2011). Of these variables,  $L_T$  had the greatest influence here. But, unlike for many other teleosts (discussed by Grixti *et al.*, 2010b), including the sparids, *A. australis* (Butcher *et al.*, 2008), *C. laticeps* (Götz *et al.*, 2007), *D. annularis* (Alós *et al.*, 2008) and *S. aurata* (Veiga *et al.*, 2011) and, contrary might be considered intuitive, hook ingestion was biased towards smaller *P. auratus* (Fig. 1).

The few data mean that the above relationship between anatomical hook location and  $L_T$  should be treated with caution. Nevertheless, one plausible explanation is that even though the lines were actively fished, smaller fish may have been able to consume baits before the anglers could detect their presence, which could have allowed some of them to be hooked more deeply. Additional trials would be required to validate this hypothesis and to more closely investigate the importance of other, more controllable, factors affecting hook ingestion so that coherent mitigation strategies can be implemented. In particular, previous studies have shown that changes to terminal rigs, including larger hooks and or subtle modifications (*e.g.* Butcher *et al.*, 2008) are effective in promoting mouth hooking among sparids (Butcher *et al.*, 2008; Alós *et al.*, 2009b; Grixti *et al.*, 2010b).

Irrespective of any modifications to terminal rigs to increase mouth hooking, a concomitant strategy that also should be promoted is to release all hook-ingested fish with their line cut (Broadhurst *et al.*, 2007; Butcher *et al.*, 2007; Alós *et al.*, 2009a; Grixti *et al.*, 2010a). Broadhurst *et al.* (2007) and Butcher *et al.* (2007) demonstrated that such a practice was appropriate for improving the fate of *A. australis*, with up to 85% of line-cut hook-



337 ingested individuals surviving (over up to three months); most of which subsequently ejected  
338 their hooks. More recently, McGrath *et al.*, (2011) observed 25% mortality among 108 hook-  
339 ingested *P. auratus* monitored in aquaria tanks for six weeks, with 77% of survivors ejecting  
340 their hooks over an average of *c.* 9 days. By comparison, there were 100% fatalities among  
341 fish ( $n = 3$ ) that had their ingested hooks removed here.

342  
343 The results from this study indicate minimal post-release mortalities to *P. auratus* after  
344 being angled and released during conventional fishing in shallow water. Furthermore, the  
345 impacts to survivors appeared to be fairly limited with few differences in blood plasma  
346 glucose and cortisol between treatments and controls at the end of monitoring, and  
347 immediately sampled wild-caught individuals. Both parameters (across all groups) were  
348 within the ranges for unstressed *P. auratus* (*e.g.* Cleary *et al.*, 2000). However, these data are  
349 limited to the conditions examined. Like several other sparids (*e.g.* *C. laticeps* – Götz *et al.*,  
350 2007, *D. annularis* – Alós *et al.*, 2009a; and *P. pagrus* – Stephen & Harris, 2010) larger *P.*  
351 *auratus* inhabit deeper water, where they are extensively targeted by anglers. In addition to  
352 any impacts of terminal rigs, are the ancillary effects of barotrauma. This factor has been  
353 implicated as contributing towards high mortalities among angled *C. laticeps* (Götz *et al.*,  
354 2007) and *P. pagrus* (Stephen & Harris, 2010), and trap-caught *P. auratus* (Stewart, 2008).

355  
356 Clearly, the occurrence of barotrauma, along with associated impacts and methods by  
357 which these might be mitigated for angled *P. auratus*, need to be assessed to more  
358 comprehensively describe the post-release fate of this species and facilitate its future  
359 management. Based on the uniformity among known factors affecting the mortality of  
360 sparids angled-and-released from shallow water, it is likely that any such assessments would  
361 have broader application across the entire family.

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485

TABLE I. Summary of categorical and, where applicable, mean ( $\pm$  S.D.) continuous random and fixed ('terminal-rig', 'fishing-and-landing' and 'angling-response') factors collected for the live and dead angled-and-released *Pagrus auratus*. <sup>1</sup>seven fish died immediately and were not caged.

Variables	Alive	Dead
<i>Design/random factors</i>		
Angler		
1	20	5
2	21	0
3	20	0
4	16	4
5	18	0
6	11	1
7	11	1
8	8	0
9	7	1
10	6	0
11	3	0
12	1	0
13	1	0
14	1	0
15	1	0
Cages <sup>1</sup>		



511	110-l individual	69	4
512	110-l mixed 1	10	0
513	110-l mixed 2	5	0
514	110-l mixed 3	4	0
515	110-l mixed 4	4	0
516	110-l mixed 5	4	0
517	110-l mixed 6	3	0
518	110-l mixed 7	2	0
519	110-l mixed 8	2	0
520	110-l mixed 9	2	0
521	2600-l mixed 1	19	0
522	2600-l mixed 2	18	0
523	2600-l mixed 3	3	0
524			
525	<i>Terminal-rig factors</i>		
526	Hook type		
527	J	98	7
528	Circle	46	5
529			
530	Absolute hook size (mm <sup>2</sup> )	312.7 (117.0)	356.4 (65.9)
531			
532	Line strength (kg)	2.8 (0.7)	2.6 (0.6)
533			
534	Trace length (cm)	73.2 (42.9)	63.6 (24.4)
535			

536	Bait type		
537	<i>Trachurus</i> sp	10	0
538	<i>Mugil cephalus</i>	7	0
539	<i>Sardinops neopilchardus</i>	11	0
540	<i>Metapenaeus macleyi</i>	58	6
541	<i>Loliginidae</i>	59	6
542			
543	Rig type		
544	Hook only	36	5
545	>50-cm trace	33	2
546	<50-cm trace	14	0
547	Paternoster	50	5
548	Sinker on hook	5	0
549			
550	<i>Fishing-and-landing factors</i>		
551	Fishing method		
552	Anchored	86	5
553	Drifting	59	7
554			
555	Fishing depth (m)	7.4 (2.2)	7.3 (2.2)
556			
557	Playing time (s)		
558	<10	63	5
559	11–30	79	7
560	31–60	2	0

561	>61	1	0
562			
563	Landing method		
564	Knotless net	2	0
565	Knotted net	4	0
566	No net	139	12
567			
568	Restraint method		
569	Dry bare hand	26	1
570	Wet bare hand	117	11
571	Towel	1	0
572	Not restrained	1	0
573			
574	Air exposure (s)		
575	<15	41	3
576	16–30	98	7
577	31–60	5	2
578			
579	Hook removed		
580	No	5	6
581	Yes	140	6
582			
583	<i>Angling response factors</i>		
584	Hook location		
585	Ingested	5	9

586	Mouth	140	2
587	Body	0	1
588			
589	Hook damage		
590	No	137	10
591	Yes	8	2
592			
593	Bleeding		
594	No	137	8
595	Yes	8	4
596			
597			

TABLE II. Wald- and deviance-derived  $P$ -values, and variance component ratios for the random effect of angler, associated with fixed variables tested in generalized linear mixed models (GLMMs) for their independence on the mortality of angled-and-released *Pagrus auratus*. Two groups of models were applied: the first to just the terminal-rig and fishing-and-landing variables; and the second to only those data describing the angling responses of fish.  $L_T$  was fitted as a co-variate in all GLMMs, and in all cases returned  $P(\text{Wald})$  and  $P(\text{deviance}) > 0.05$ .

Variables	$P$		Variance component ratio
	Wald	Deviance	for angler
<i>Terminal-rig and fishing-and-landing GLMMs</i>			
Hook type	0.980	0.695	1.711
Absolute hook size	0.480	0.246	0.692
Line strength	0.696	0.418	1.597
Trace length	0.499	0.466	1.539
Bait type	0.879	0.298	2.868
Rig type	1.000	0.342	2.145
Playing time	0.999	0.917	1.516
Water depth	0.447	0.921	1.883
Fishing method	0.279	0.171	1.523
Landing net	0.991	0.623	1.266
Restraint method	0.976	0.746	1.404
Air exposure	0.132	0.382	2.308
Hook removed	0.000	0.000	0.412

623

624     *Angling-response GLMMs*

625	Hook location	0.000	0.000	0.210
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626	Hook damage	0.146	0.192	1.407
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627	Bleeding	0.004	0.006	1.478
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628

TABLE III. Wald- and deviance-derived  $P$ -values, and variance component ratios for the random effect of angler, associated with fixed variables tested in generalized linear mixed models for their independence on the anatomical hook location of angled *Pagrus auratus*

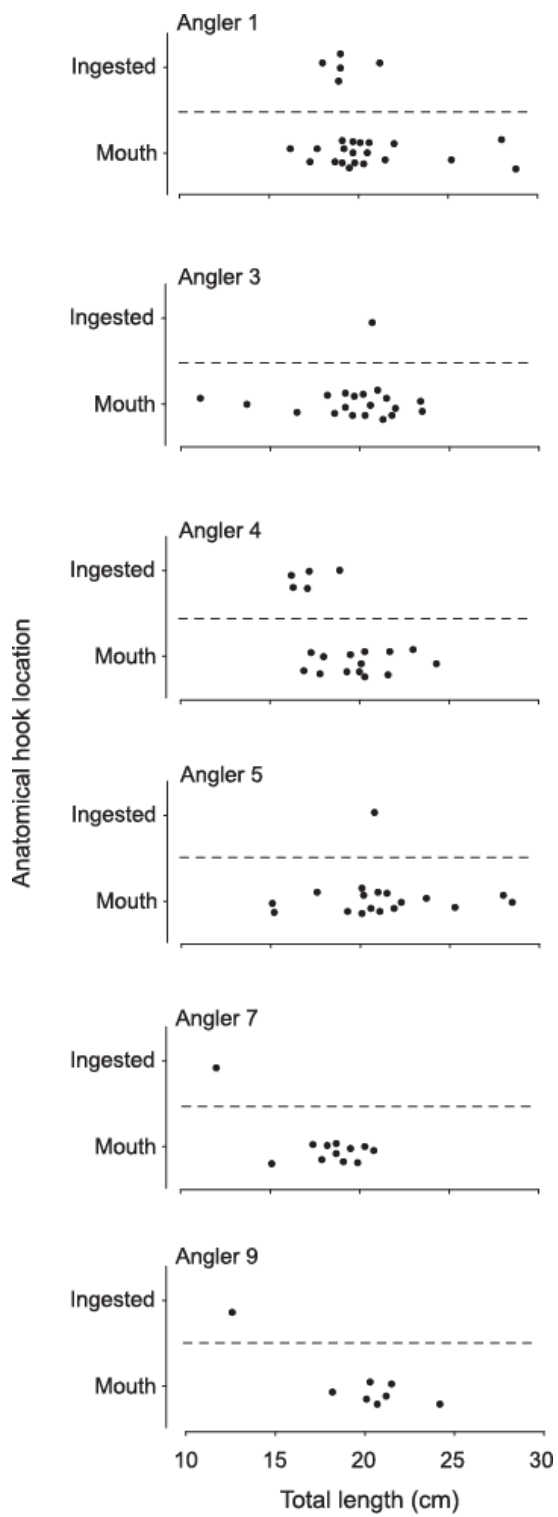
Variables	$P$		Variance component ratio
	Wald	Deviance	for angler
Hook type	0.904	0.653	0.768
Absolute hook size	0.868	0.673	0.340
Line strength	0.541	0.352	0.708
Trace length	0.992	0.611	0.938
Bait type	0.927	0.454	1.545
Rig type	0.856	0.105	0.537
$L_T$	0.046	0.501	1.617

644     **Caption to Fig**

645     Fig. 1. Jitter plots of the total length of *Pagrus auratus* v. anatomical hook location for each of the  
646     six anglers that caught hook-ingested fish.

647





648